CHROMOSOME NUMBERS AND THE ANATOMY OF THE SECONDARY XYLEM IN THE OLEACEAE

KARL SAX AND ERNST C. ABBE

With two text figures

THE OLEACEAE form a natural family of plants, although there are well marked differences between most of the genera. The family is divided into the Oleoideae which includes *Fraxinus*, *Forsythia*, *Syringa*, *Forestiera*, *Chionanthus*, *Olea*, and *Ligustrum*, and the subfamily Jasminoideae which includes *Jasminum*. According to Rehder there are more than 20 genera with over 400 species, most of which are trees and shrubs.

The natural grouping of these genera is indicated not only by their taxonomic characters but also by their immunological, grafting, and anatomical relationships. Chester (1931) working with *Chionanthus*, *Fraxinus*, *Forsythia*, *Ligustrum* and *Syringa*, found no normal precipitin reactions between these genera.

According to DeCandolle the Lilac can be grafted on Ash, *Chionanthus* and *Fontanesia* while the Persian Lilac grafted on *Phillyrea* survived for ten years. The Olive can also be grafted on *Phillyrea* and *Fraxinus*. *Syringa* is commonly grafted on Ligustrum stock, although as Chester has pointed out, this practice often leads to "graft blight" due to incompatibility between stock and scion. The writer has seen Syringa grafts on *Fraxinus* which made a growth of several feet, but the graft does not survive the second year. These grafts were made by Dr. Johnson in Illinois. Chester found complete incompatibility of grafts between *Syringa* with *Chionanthus* and *Forsythia*. The fact that such morphologically diverse genera as *Syringa* and *Fraxinus* will function together, even for one season, indicates a rather close relationship between these genera.

The Oleaceae are widely distributed and are found in Asia, Europe, and America. Certain genera such as *Fraxinus* and *Chionanthus* are represented in both North America and Asia, while others such as *Syringa*, *Forsythia* and *Ligustrum* are natives of Asia and Europe. One genus, *Forestiera*, is found only in North and South America. The geographic distribution indicates that the family originated in Asia.

The relationships of the genera of Oleaceae would indicate that the chromosome complexes might be similar. Little cytological work has been done on this family. The writer (Sax, 1930) found 23–34 pairs of chromosomes in representative species of *Syringa*,

and Tischler (1930) reports 22 chromosomes for this genus. O'Mara (1930) found 14 pairs of chromosomes in *Forsythia*. The chromosome numbers of other genera available in the Arnold Arboretum have been investigated. The meiotic counts are based on aceto-carmine smear preparations. The writer is indebted to Mr. Dermen for the preparations of *Ligustrum*, *Olea* and *Jasminum*. Most of the chromosome counts for *Syringa* are based on the writer's earlier study of this group. The haploid chromosome numbers of the species studied are presented in the following table. The counts for *Olea* and *Jasminum* are based on preparations of root tips obtained from plants in the greenhouse.

Oleaceae

Genus	Species	Chromosome No.	Habitat
Fraxinus	Sec. 1. Bungeana	23	China
	chinensis	69	Asia
	Sec. 2. americana	23	N. America
	pennsylvanica	23	N. America
	oregona	23	N. America
	excelsior	23	Eu., Asia Minor
Forsythia	suspensa	14	China
	viridissima	14	China
	europaea	14	S. E. Europe
	ovata	14	Korea
Syringa Subgen. 1. Ser. 1.	yunnanensis	24–68	China
	Josikaea	23	S. E. Europe
	Sweginzowii	23	China
	villosa	23–24	China
	tomentella	23–24	China
	Komarowi	23	China
Syringa Ser. 2.	velutina	23	Asia
	Palibiniana	24	Korea
	pubescens	24	China
	Meyeri	23	China
	oblata Giraldii	23–24	China
	vulgaris (varieties)	23–24	S. E. Europe
	persica laciniata	22	China
	pinnatifolia	24	China
Subgen. 2.	amurensis	23	China
	japonica	23	Japan
Forestiera	acuminata	23	N. America
Chionanthus	virginica	23	N. America
Ligustrum	vulgare	23	Eu., N. Afr.
	Quihoui	23	China
	acuminatum	23	Japan

Genus	Species	Chromosome No.	Habitat
	ibota	23	Japan
	acutissimum	23	China
	amurense	23	China
	obtusifolium	23	Japan
Olea			
	europaea	23	S. Europe
Jasminum			
	fruticans	13	Mediterr. Reg.

The basic haploid chromosome number in *Fraxinus* is 23. One of the bivalent chromosomes seems to be conspicuously larger than the others, a situation also found in several other genera of this family. *Fraxinus chinensis* is a hexaploid with about 69 pairs of chromosomes. As shown in figure 2 there is no great amount of secondary pairing of the meiotic chromosomes.

All of the species, varieties and species hybrids of *Forsythia* have 14 pairs of chromosomes (O'Mara). The somatic chromosomes of *F. intermedia* are shown in figure 11. The size and shape of the somatic chromosomes are essentially the same as those of *Syringa* (Sax 1930), *Fraxinus* and *Olea*.

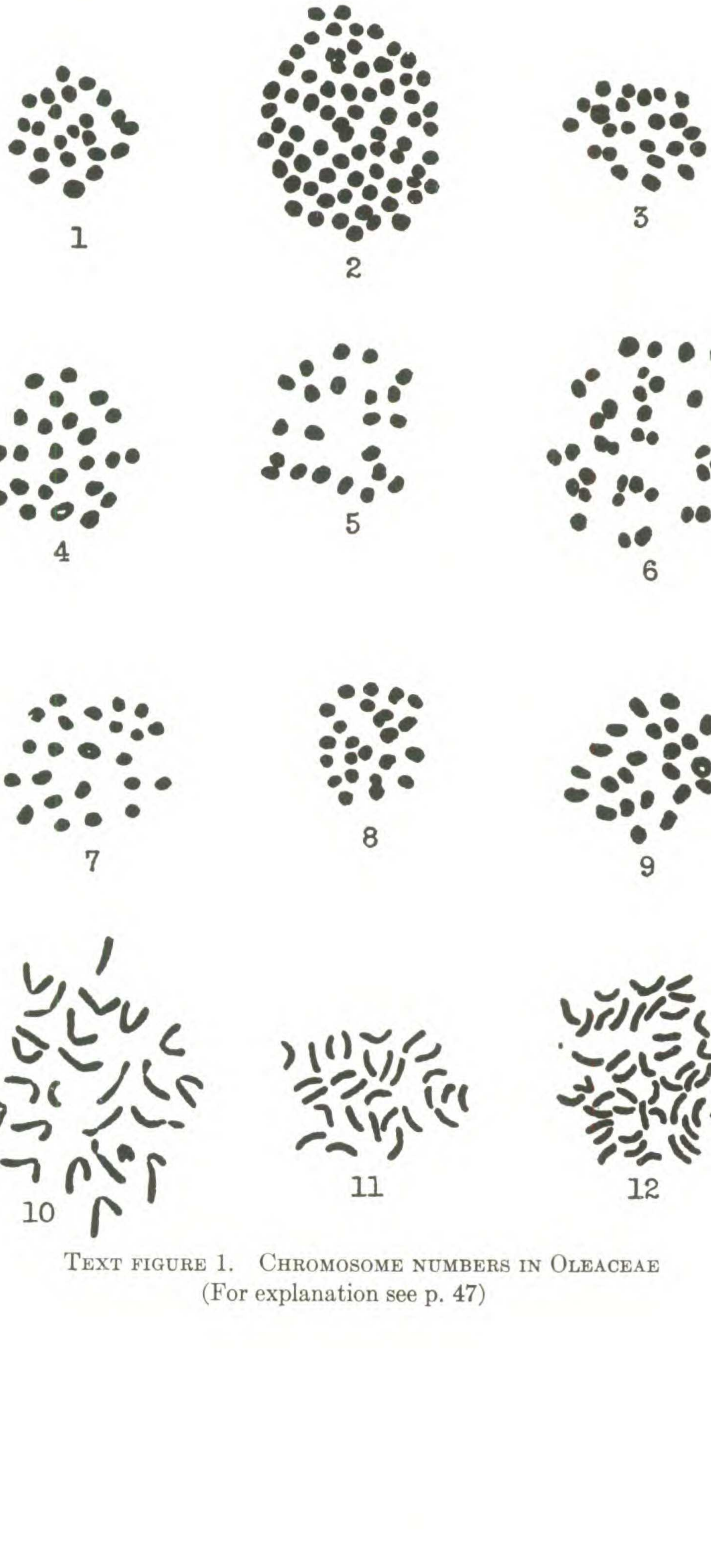
The chromosome number in *Syringa* seems to vary somewhat. Tischler (1930) reports 22 meiotic chromosomes in several species. The writer has found 22 pairs of chromosomes in *S. persica lacinata* (a fertile form from China), but 23 is the number most frequently found in the other species.

In the species hybrid *S. chinensis* (*S. persica* × *S. vulgaris*) there are usually about 24 chromosomes at meiosis but in some cases the number at metaphase may be 36 (fig. 6) or more. In some division figures there seems to be about 12 bivalents and 12 univalents (Sax 1930) which would indicate that one of the parents contributed only 12 chromosomes in this cross. But both *S. vulgaris* and the fertile forms of *S. persica laciniata* have about 23 pairs of chromosomes.

Syringa persica and some of its varieties are also species hybrids as shown by the writer and by Tischler. The chromosome behavior is irregular and the plants are highly sterile. In some cases as many as 44 chromosomes have been counted at meiosis. It is probable that there is weak pairing of the chromosomes in these hybrids so that only univalent chromosomes are sometimes found at meiosis.

The haploid chromosome number is 23 for *Forestiera*, *Chionanthus* and *Ligustrum* (figs. 7, 8 and 9). There are 46 somatic chromosomes in *Olea europaea* which are similar to those of *Syringa* and *Forsythia* in respect to size and shape.

Jasminum has been placed in the subfamily Jasminoideae. The one species studied, *J. fruticans*, has 26 somatic chromosomes. As



TEXT FIGURE 1. CHROMOSOME NUMBERS IN OLEACEAE

(For explanation see p. 47)

shown in Figure 10, the somatic chromosomes are somewhat longer than those of the genera in the first group. The chromosome number and morphology in this genus seems to support the taxonomic grouping of this genus in a second subfamily.

Of the 8 genera studied 6 have 23 chromosomes as the basic number. It is possible that the original basic number was about 12, since *Forsythia* has 14 pairs of chromosomes and *Jasminum* has 13. There is also some evidence that in the species hybrid *S. chinensis* there may be approximately 12 bivalent and 12 univalent chromosomes at meiosis.

In general the genera and species of Oleaceae seem to constitute rather distinct genetic units. The only generic hybrid known is between *Osmanthus* and *Phillyrea* which was mentioned in a recent issue of Gardener's Chronicle (ser. 3, XC. 367. 1931). A few species hybrids are found in *Forsythia*, *Syringa* and *Ligustrum*. Numerous attempts have been made to cross species from different groups of the genus Syringa but without success.

The Oleaceae have been differentiated into rather well marked genera and species and have attained a wide geographic distribution with little change in chromosome number or chromosome morphology.

ANATOMY OF THE SECONDARY XYLEM

Before discussing the groups into which the genera under consideration naturally fall, it might be well to give a short description of each genus. The genera[1] studied are described in the order in which they are represented in Figure 2, (p. 46) reading up.

The material of *Jasminum*[2] available being only one year old, the conclusions based on it later are presented as being only tentative. The rays are uniformly uniseriate, and are composed of vertically elongate cells. Kohl (1881 p. 6) states that in more mature material they are rarely biseriate, and generally composed of vertically elongate or isodiametric cells (*J. revolutum*) only. The segments of the thin-walled, angular vessels have acute and porous end walls and gradually decrease in diameter in the course of the season's growth, so that a simple type of ring-porosity obtains. Parenchyma is both terminal and associated with the vessels. The tracheid walls are of medium thickness with rather large bordered pits whose orifices are not as long as the diameter of the pit membrane. Tertiary spiral thickening of the walls is present in both vessels and tracheids.

Forsythia,[3] as well as the remaining genera, commonly has both

[1] The junior author had access to Professor I. W. Bailey's collection of slides, augmented by material kindly supplied by Alfred Rehder and Professor Record.
[2] Represented by *J. heterophyllum* Roxb. and *J. Giraldii* Diels.
[3] Represented by *F. suspensa* Vahl, and *F. viridissima* Lindl.

multiseriate and uniseriate rays. The multiseriates in this genus are commonly two cells wide, and have uniseriate extensions which are longer than those in the other genera studied. The marginal cells are tall, although often also isodiametric in the radical plane. In arrangement the vessels are diffuse or weakly ring-porous and are mostly solitary. less often in radial groups of two or three, rarely in larger radial groups. In structure the vessel segments are thin-walled, angular, elongate, with acute end walls which are occasionally scalariform or tend to retain vestiges of bars when porous. The parenchyma occurs as isolated cells between the vessels, directly associated with the vessels, and also terminal. The tracheid walls are of medium thickness and have large bordered pits with short diagonal orifices. Both vessels and tracheids have spiral tertiary thickening.

The uniseriate rays in *Syringa*[1] are generally accompanied by biseriate rays although triseriates occur commonly in *S. Julianae* and *S. yunnanensis*. Uniseriate extensions may occur in the *Vulgares* group but are practically absent in the other two groups. The marginals are usually isodiametric in the radial plane, with a tendency towards their being vertically elongate in the species which have the longer uniseriate extensions. In the *Ligustrinae*, on the other hand, horizontally elongate marginals are more common. The vessel segments are elongate, thin-walled, angular with acute to obtuse end walls which are generally porous, although Solereder (1885, p. 171) reports having found scalariform end walls with a single bar in *S. vulgaris*.

Although the bulk of the species are ring-porous and have spiral thickenings in the tracheids and vessels, the members of the *Ligustrinae* have diffuse vessel arrangement, only very weak spiral thickening, and, in addition, have tyloses in the vessels.

The walls of the spring tracheids range from rather thin to medium thick, while in the summer wood they are medium thick to thick. The pits are bordered and have elongate, diagonal orifices which are as long or somewhat longer than the diameter of the pit membrane.

Both uniseriate and biseriate or triseriate rays are present in *Ligustrum*,[2] but uniseriate extensions are seldom present and are very short when they do occur. The marginal cells vary from isodiametric to vertically elongate. The angular, thin-walled vessels

[1] Represented in subgen. *Eusyringa* group *Villosae* by *S. yunnanensis* Franch., *S. villosa* Vahl; in *Eusyringa* group *Vulgares* by *S. Julianae* Schneid., *S. microphylla* Diels, *S. persica* L., *S. pinnatifolia* Hemsl., *S. pubescens* Turcz., *S. velutina* Komar.; in subgen. *Ligustrina* by *S. amurensis* Rupr., *S. japonica* Decne., *S. pekinensis* Rupr.

[2] Represented by *L. kiyozumianum* Nakai, *L. sinense* Lour., *L. vulgare* L.

have elongate segments with acute to obtuse, porous end walls. They are ring-porous in arrangement, most commonly occurring alone or in radial groups of two or three, or in long radial or diagonal rows (*L. sinense*).

The parenchyma is sparse and is only terminal or next to vessels.

The tracheids are medium to thick-walled and have bordered pits with orifices about as long or longer than the diameter of the pit membrane.

Associated with the uniseriate rays in *Chionanthus*[1] are bi-, tri-, and rarely 4- or 5-seriate rays which ordinarily completely lack uniseriate extensions, but may have short ones. The marginals are isodiametric or even horizontally elongate in the radial plane. The vessel segments are elongate, thin-walled, angular, and have acute end walls which are porous. The vessels occur in diagonal groups, forming "flames," the component vessels decreasing in size in the course of the year's growth. The wood parenchyma is terminal and also associated with the vessels. Tracheids are not very thick-walled and have bordered pits with elongate diagonal orifices about the width of the pit membrane.

The ray condition in *Fraxinus*[2] is quite variable but is predominantly fusiform associated with occasional uniseriates. The multiseriates in some cases (*F. Sieboldiana, F. Biltmoreana, F. caroliniana, F. oregona, F. mandschurica*) may have an occasional very short uniseriate extension. The multiseriate rays generally far outbalance the uniseriates in number but *F. caroliniana* is a notable exception in this respect. The marginal cells are ordinarily horizontally elongate with a strong tendency especially in the *Melioides* toward the isodiametric type.

The vessel segments are of two types, the thick-walled, elongate ones of small diameter with obtuse to acute porous end walls, and the thin-walled, depressed segments with transverse porous end walls, relatively great diameter (4 or 5 × that of the later summer wood vessels). Both types occur singly or in radial pairs or groups of 3 or 4. The thick-walled vessels characterize the summer wood, and the thin-walled ones the spring wood. There is ordinarily a very rapid transition from the spring to the summer type of vessel resulting in a very definite ring-porous condition.

The parenchyma occurs both with the vessels and terminally,

[1] Represented by *C. virginica* L.

[2] Represented in § Ornus by *F. pubinervis* Bge., *F. chinensis* Roxb. var. *rhynchophylla* Hemsl., *F. floribunda* Wall., *F. Sieboldiana* Blume; in § *Fraxinaster* by *F. americana* L., *F. Biltmoreana* Beadle, *F. oregona* Nutt., *F. carolinana* Mill., *F. pennsylvanica* Marsh.; in § Melioides by *F. mandschurica* Rupr., *F. quadrangulata* Michx., *F. nigra* Marsh.

with a strong tendency toward the formation of tangential bands in the summer wood.

The tracheids are thin-walled in the spring wood and thicker in the summer wood, having in both cases bordered pits with orifices as long as or longer (much longer in the summer wood) than the diameter of the pit membrane.

Tyloses generally fill the lumens of the vessels.

Forestiera[1] has both uniseriate and biseriate rays, the biseriate rays sometimes often lacking uniseriate extensions which do not average as long as in *Forsythia*. The marginal cells are much more rarely vertically elongate than in *Forsythia*, tending more commonly to be isodiametric in the radial plane of section. The vessels are diffuse in arrangement, occurring singly, or in pairs, less commonly in radial groups of three or rarely four. The rather thick-walled vessel segments are elongate with obtuse, porous end walls. Parenchyma is terminal and also associated with the vessels with a tendency toward tangential groups in *F. rhamnifolia* and well developed tangential rows in *F. porulosa*. The pitting of the rather thick-walled tracheids is typically bordered with the mouth of the pit varying in size from slightly less than to several times the diameter of the pit membrane.

In *Olea*[2] the multiseriate rays vary from bi- to triseriate, and are always associated with small uniseriates. Except in *O. europaea* which often has fairly long uniseriate extensions on the rays, they are fusiform. The marginal cells range from slightly elongate vertically to isodiametric in *O. europaea*, but in the other species they are more commonly isodiametric to horizontally elongate. The elongate, rather thick-walled vessel segments with porous and obtuse end walls, occur singly or in groups of several to many. These groups are simply radial rows in *O. europaea*, but in the other two species they tend to be in "flames." Parenchyma is in tangential bands in *O. Cunninghamii* and *O. verrucosa* as well as being associated with the vessels in the "flames." In *O. europaea*, however, it is simply terminal and beside the vessels. Tracheids are very thick-walled and the pit mouths are very elongate or simply porous.

The above descriptions are summarized and generalized in a diagrammatic form in Fig. 1.

Jasminum with its uniseriate or rarely biseriate rays composed of vertically elongate cells stands well apart from the other genera studied which uniformly have very well developed multiseriate as well as uniseriate rays. The tracheid-like vessel segments of *Jas-*

[1] Represented by *F. acuminata* Poir., *F. neo-mexicana* Gray, *F. porulosa* Poir., and *F. rhamnifolia* Griseb.

[2] Represented by *O. europaea* L., *O. Cunninghamii* Hook., and *O. verrucosa* Link.

minum also distinguish it. In both rays and vessel structure *Forsythia* approaches *Jasminum* more closely than do any other genera of the Oleideae. On the other hand, *Forsythia* differs in such important respects as type of parenchyma distribution, the occasional occurrence of vessel segments with scalariform end walls, and ring porous vessel distribution. Nevertheless, the anatomical structure of *Jasminum* is closer to that of *Forsythia* than that of the other genera, a conclusion also reached by Kohl (1881). That the chromosome numbers of the two is so close is very suggestive, although there is not a complete parallelism because morphologically *Forsythia* seems to approach *Syringa* more nearly than it does *Jasminum*.

In the Oleoideae, *Forsythia* resembles in its diffuse vessel distribution the members of the Ligustrinae in *Syringa*. The reported occurrence of weakly scalariform end walls in *Syringa* strengthens this similarity. Although similar to *Syringa* in these respects it differs in type of parenchyma distribution, and has much longer uniseriate extensions on the multiseriate rays. Thus, although showing many points of similarity to *Syringa*, *Forsythia* is distinguished by the rather commoner occurrence of a decadent scalariform type of end wall, parenchyma between the vessels, and diffuse vessel distribution. That the chromosome number of *Forsythia* is different from that of all the other Oleoideae is of interest, considered in connection with its grafting incompatibility with other genera of this subfamily.

Although *Syringa* has several tendencies in common with *Forsythia*, it shows much closer similarity to *Ligustrum* which in turn is quite close in structure to *Chionanthus*. This grouping is significant because although DeCandolle states that Lilac can be grafted on *Chionanthus*, Chester finds incompatibility of such grafts after the first year. The vessels are of the same type in the three genera, the chief variation being found in vessel arrangement which varies in *Syringa* from diffuse to ring-porous, is ring-porous in *Ligustrum*, and in "flames" in *Chionanthus*. Associated with reduction of length is the decreased occurrence of uniseriate extensions of the multiseriate rays, as well as a tendency toward horizontally rather than vertically elongate marginal cells. Although *Chionanthus* and *Syringa* stand at opposite ends of this range variation, it is so continuous that they appear to be components of the same complex.

Another natural group is formed by *Olea europaea* and *Forestiera*, with their thick-walled, unevenly thickened vessels which tend to occur uniformly in distinctive groups of two or three throughout

TEXT FIGURE 2. ANATOMY OF THE SECONDARY XYLEM IN OLEACEAE
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the growth ring. The rays, as well as the parenchyma, are essentially of the Ligustrum type, although in the parenchyma there is a tendency toward the formation of tangential rows.

Fraxinus stands very much alone, although it has characters suggesting each of the two previous groups. In the ray type and the ring-porous condition it strongly suggests the Syringa-Ligustrum-Chionanthus complex. In parenchyma, and vessel distribution in the summer wood, it resembles the Olea-Forestiera group. And making it quite distinct from either group is the occurrence in the spring wood of the very large, thin-walled vessel segments with their transverse, porous end walls. In its chromosome number and morphology it is the same as the other two groups, and by its grafting relationships it shows an affinity for each group.

On the whole there is a suggestive parallelism between chromosome number, grafting relationships and anatomical structure.

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Cytological Laboratory, Arnold Arboretum
Harvard University.

DESCRIPTION OF FIG. 1

The meiotic figures are from aceto-carmine mounts. Magnification 2000 ×. The somatic chromosomes from root tip preparations are magnified 4000 ×.

1. Fraxinus excelsior. 1 M. 23 chromosomes.
2. Fraxinus chinensis rhynchophylla. 1 M. 69 chromosomes.
3. Fraxinus pennsylvanica. 1 M. 23 chromosomes.
4. Syringa vulgaris var. 1 M. 24 chromosomes.
5. Syringa persica laciniata. 1 M. 22 chromosomes.
6. Syringa chinensis Saugeana. 1 M. 36 chromosomes of which about 12 are univalents.
7. Foresteria acuminata. 1 M. 23 chromosomes.
8. Chionanthus virginica. 1 M. 23 chromosomes.
9. Ligustrum amurensis. 1 M. 23 chromosomes.

10. Jasminum fruticans. 26 somatic chromosomes.
11. Forsythia intermedia. 28 somatic chromosomes.
12. Olea europaea. 46 somatic chromosomes.

DESCRIPTION OF FIG. 2

Diagrammatic comparison of the wood structure of the genera examined. M = parenchyma between the vessels and associated with the vessels as well as terminal; P = parenchyma terminal and associated with the vessels; Pt = parenchyma terminal and associated with the vessels and forming tangential rows in the summer wood. The rectangles on the right hand side of each multiseriate ray indicate the aspect of the marginal cells in the radical plane. Uniseriate rays and uniseriate extensions of multiseriate rays are indicated in solid black.